

The Distribution and Ecology of Epigeic Invertebrates on the Subantarctic Island of South Georgia

By Michael Vogel

Philipps Universität Marburg

Abstract

Collections of arthropods on the subantarctic island of South Georgia during the austral summers 1980/81 and 1981/82 showed that it is best regarded as an "archipelago" consisting of several biogeographical "islands" rather than a single biogeographical unit. The composition of the epigeic invertebrate fauna of nine areas including tussock stands, grass-heath communities and marsh-bog formations in Cumberland East Bay differs in quantity rather than quality. Only a few epigeic arthropods are strictly limited to specific areas. The carabid and staphylinid beetles inhabit warmer lowland areas and the lathridiid beetle inhabits *Poa flabellata* heads infected with fungi. The only parasitic hymenopteran, *Notomyrma aptenosoma*, is rare and parasitizes eggs of perimylopod beetles. These beetles



Figure 1: Invertebrate study areas on South Georgia.

are the most important insects in the terrestrial ecosystems of South Georgia, both because of their absolute numbers and their role as decomposers. The ratio of parasitic/carnivorous arthropods to the rest of the winged insects was found to be 1:12.3. As predatory forms only the spiders may be of quantitative importance and their proportion of the total epigeic invertebrate fauna was 13–36%.

Introduction

The faunal composition and the structure and function of arctic tundra ecosystems is relatively well known (see REMMERT 1980). The pollination of flowers is achieved by flies, whereas Hymenoptera and Lepidoptera play a minor role – with the spectacular exception of *Bombus*. The degradation of plant material is not carried out by ectothermic herbivores but by decomposers which are Diptera, usually sciarids and mycetophilids. Predators are made up by spiders (Linyphiidae and Micryphantidae) and parasitic Hymenoptera. For the antarctic and subantarctic region there exist several systematic accounts but almost no ecological data to make a bi-polar comparison possible. Therefore the epigeic invertebrate fauna of South Georgia was studied.

The subantarctic island of South Georgia stretches from north-west to south-east between 38°58' – 38°W and 53°58' – 54°53' S. It is about 2 000 km east of the southern tip of South America. The island is approximately 170 km long and 5–35 km wide with a total land area of about 3 750 km². The island is mountainous, a large part being permanently covered with ice and glaciers flow into the sea (GRESSITT 1970; SMITH & WALTON 1975). The island is divided into several "oasis", separated by these glaciers, mountains and the sea (Fig. 1). Three of these "oases" were studied: Husvik (Busen Peninsula/Stromness Bay), Grytviken (Cumberland East Bay) and Royal Bay. Between these places there are characteristic faunal differences (see Table 1). At Husvik *Trechisibus antarcticus* replaces *Oofterus soledadinus* (Coleoptera, Carabidae), and instead of the spider *Perimaso grytvikensis* we found *Hilaira* sp. A similar exchange was found between ephydrid and dryomyzid flies. The lathridiid beetle *Aridius malouinensis* and a terrestrial snail (SMITH & WALTON 1975) occurred only in Cumberland East Bay. Most of these species are absent in Royal Bay, but there is (instead of the spider *Neomaso claggi*) a new *Notiomaso* species. Similar patterns of distribution are demonstrated by several plant species. Many of them do not occur in Royal Bay (e. g. *Alopecurus antarcticus*, *Ranunculus repens*, *Cystopteris fragilis*, *Polystichum mohroides* and *Lycopodium magellanicum*). On the other hand, the fern *Blechnum penna-marina* is found only near Husvik (after GREENE 1964). Because of these differences we confined our studies to the Grytviken area in Cumberland East Bay.

Material and methods

During January 1981 and January – February 1982 we set out pitfall traps in different biotopes of Cumberland East Bay, around the research station of the British Antarctic Survey at King Edward Point. Pitfall traps provide collections representative of the surface-active invertebrate fauna of an area. Each trap contained a mixture of formaldehyde (7%), water and a detergent. Ten traps were placed at a distance of 2 m from each other at each sampling site. The minimum capture time was 12 days in 1981 and 33 days in 1982. In 1981 we collected 11 360 animals, in 1982 60 757 animals. The invertebrates were preserved in alcohol, then counted and examined. The results from 1982 are presented in this paper because of the greater number of specimens.

Results

The plant communities of South Georgia and their invertebrate populations

According to GREENE (1964) the vascular flora of South Georgia may be classified into three main groups of plant communities which among themselves also contain unique subcommunities. The main groups are: 1. Tussock Communities; 2. Grass-Heath Communities; and 3. Marsh-Bog Communities.

1. Tussock Communities

Poa flabellata, the tussock grass, grows best in coastal regions but is also found at elevations up to 300 m. The plants are so dense in some areas that subsequent tussock formation and growth of other plants are prevented. Thus a “closed” tussock formation develops. A more widespread form is the “open” tussock community with conspicuous “stool” formation, which is found mostly in coastal areas frequented by vertebrates (e. g. elephant seals and penguins), and in areas with particular topographical conditions (e. g. soil movement). Since more light can reach the ground in open tussock it is possible for other plants to grow there also (GREENE 1964; SMITH & WALTON 1975; LAWS 1978). In general the above-ground production of tussock communities is very high (up to 5000 g/m²/year).

We chose two distinct types of open tussock grassland for the investigations.

1.1 Open, wet coastal tussock. The site was located behind the station of the British Antarctic Survey at King Edward Point, in the direction of the old whaling station. It was approximately 3 m above sea level. The traps were placed on the border area between the tussock grassland and a meadow. Some of the tussocks have been uprooted by passage of elephant seals. Between the tussocks puddles and seal wallows are found and in some places *Acaena magellanica* and *Deschampsia antarctica* grow in clumps. The transition area from the tussock grassland to meadow is not abrupt, but rather a mosaic of the two communities. The vegetation in the meadow consists mainly of *Poa annua* and *Agrostis tenuis* with clumps of *Acaena magellanica*. *Juncus* sp. is found in shallow puddles in this area.

1.2 Open, dry slope tussock. This site was located across the bay from the station at Susa Point. It was approximately 40 m above sea level and faced north-east. *Poa flabellata* grows here in a more tuft-like

Table 1: Distribution of selected species and groups in three colonization areas; Husvik (Busen Peninsula/Stromness Bay), Grytviken (Cumberland East Bay) and Royal Bay.

			Husvik	Grytviken	Royal Bay
COLEOPTERA	Carabidae	<u>Ooapterus soledadinus</u>	-	+	-
		<u>Trechisibus antarcticus</u>	+	-	-
	Lathridiidae	<u>Aridius malouinensis</u>	-	+	-
DIPTERA	Ephydriidae		-	+	-
	Dryomyzidae	<u>Paractora rufipes</u>	+	-	-
THYSANOPTERA	Thripidae	<u>Apherothrips secticornis</u>	+	+	-
ARACHNIDA	Araneae	<u>Notiomaso australis</u>	+	+	+
		<u>Neomaso claggi</u>	+	+	-
		<u>Perimaso grytvikensis</u>	(1)	+	+
		<u>Hilaira sp.</u>	+	-	-
		<u>Notiomaso sp.</u>	-	-	+
ANNELIDA	Lumbricidae		+	+	-

+ = present

- = absent

(1) = present after Forster (1970) (according to collections of Jones in 1961), but not found.

Table 2: Numbers and frequencies of invertebrates collected in two tussock areas, and the calculated numbers of animals collected per day per trap (A/D/T).

			wet coastal tussock		dry slope tussock		
			no.	% TOTAL	no.	% TOTAL	
COLEOPTERA	Perimylopidae	<i>Perimylops antarcticus</i>	-	-	-	-	
		<i>P. antarcticus</i> (Larvae)	-	-	-	-	
		<i>Hydromedion sparsutum</i>	6	0.02	518	9.89	
		<i>H. sparsutum</i> (Larvae)	10	0.07	337	6.43	
	Staphylinidae	<i>Halmaeus atriceps</i>	2	0.01	-	-	
	Carabidae	<i>Oopterus soledadinus</i>	134	0.93	-	-	
	Lathridiidae	<i>Aridius malouinensis</i>	241	1.67	-	-	
DIPTERA	Trichoceridae	<i>Trichocera regelationis</i>	14	0.10	10	0.19	
		Sciariidae		252	1.75	9	0.17
		Chironomidae	<i>Parochlus steineni</i>	226	1.57	5	0.09
		Heleomyzidae	<i>Prosopantrum austrinum</i>	140	0.97	24	0.46
		Palloppteridae	<i>Heloparia ekeloefi</i>	-	-	-	-
		Ephyrididae		6953	48.22	59	1.13
THYSANOPTERA	Thripidae	<i>Aperothrips secticornis</i>	-	-	-	-	
HYMENOPTERA	Mymaridae	<i>Notomyrma aptenosoma</i>	1	0.01	11	0.21	
HEMIPTERA	Aphididae	<i>Jacksonia papillata</i>	-	-	-	-	
ARACHNIDA	Micryphantidae	<i>Notiomaso australis</i>	4098	28.49	1483	28.32	
		<i>Micromaso flavus</i>	-	-	97	1.85	
		<i>Neomaso claggi</i>	1	0.01	14	0.27	
	Acarina	not determined	468	3.25	1297	24.42	
COLLEMBOLA		not determined	1855	12.90	1373	26.22	
ANNELIDA	Lumbricidae		-	-	16	0.31	
NEMATODA		not determined	-	-	1	0.02	
TOTAL			14388		5237		
A/D/T			28.54		15.87		

fashion. Between the *Poa* plants are *Deschampsia antarctica*, *Festuca contracta*, and *Acaena magellanica*. Thick moss cushions grow under these plants. The drainage in this area is good so it is relatively dry.

Comparing the two tussock areas, one finds conspicuous differences (Table 2). In the wet coastal tussock large numbers of *Oopterus soledadinus* (Coleoptera, Carabidae) and *Aridius malouinensis* (Coleoptera, Lathridiidae) occurred. Neither of these beetles occur in the more elevated tussock stands. Investigations of other tussock areas showed that *Oopterus soledadinus* occurs only in coastal areas. In all other areas *Hydromedion sparsutum* (Coleoptera, Perimylopidae) was predominant. Probably *Oopterus* is more thermophilous and is therefore restricted to lower coastal areas. Also, being a predator, *Oopterus* seems to dwell mostly in eutrophic habitats where optimum nourishment can be found. *Hydromedion*, being a primary decomposer, prefers stands with a higher plant diversity, because in its larval stages it feeds on seedlings and roots (see WATT 1967). The lathridiid *Aridius malouinensis* was found only in coastal tussock stands. Since the Lathridiidae are fungus feeders they are associated with moist tussock containing fungal hyphae. They are also commonly found feeding on fungi (several genera) which infect *Poa flabellata*.

The Diptera fauna also reveals differences between the two tussock areas. Elephant seals, which are quite frequently found in the coastal tussock grassland, affect the fauna of this biotope drastically. Large masses of ephyridid flies occur as a result of many small, highly eutrophic pools and muddy areas. The heleomyzid flies are typically "shade-liking", vegetation colonizer, but have also be found to inhabit peoples' houses (compare JACOBS & RENNER 1974; VOGEL & NICOLAI 1983). Sciariid larvae, together with Collembola, play an important role in the decomposition of plant litter only in the coastal tussock.

Over all the research sites sciarid species were less prominent. Eutrophication of the unfavourable soil, in the coastal tussock, provided the necessary condition for their larvae. The chironomid, *Parochlus steineni*, also thrives in the very wet coastal area. Trichocerid midges inhabit soil litter as well as the underside of carcasses (see DAHL 1970) and they were found primarily in this coastal area.

The proportion of spiders found in each of the two sites was almost the same, with the exception that only *Notiomaso australis* and *Neomaso claggi* occurred in the coastal tussock. A third species, *Micromaso flavus*, was found in the slope tussock.

Both areas were found to contain generally similar species of invertebrates but in different quantities and proportions. In the coastal tussock 28.54 animals per day per trap (A/D/T) were found, in the slope tussock 15.87. The presence of annelid worms only in the slope tussock was largely because of the massive quantities of *Acaena magellanica* growing there. In general no significant differences were found between the results of the two years.

2. Grass-Heath Communities

The grass-heath communities are the most dominant of the plant communities, at least on the north-eastern coast of South Georgia. As research sites we chose at lower altitudes two "extreme areas": an *Acaena-Tortula* stand (initial stage) and an open *Festuca* grassland (final stage of development). The production in the *Acaena* stand is approximately 1 100 g/m²/year and for pure *Festuca* grassland about 800 g/m²/year (SMITH & WALTON 1975).

Table 3: Numbers and frequencies of invertebrates collected in two lowland grass-heath communities, and the calculated numbers of animals collected per day per trap (A/D/T).

		Acaena Tortula		Festuca heath Susa Point		
		№	TOTAL	№	TOTAL	
COLEOPTERA	Perimylopidae	<i>Perimylops antarcticus</i>	1	0.01	-	-
		<i>P. antarcticus</i> (Larvae)	4	0.06	-	-
		<i>Hydromedion sparsutum</i>	408	5.95	1677	28.28
	Staphylinidae	<i>H. sparsutum</i> (Larvae)	533	7.77	401	6.78
		<i>Halmaeus atriceps</i>	1	0.01	2	0.03
Carabidae	<i>Oopterus soledadinus</i>	3	0.04	-	-	
Lathridiidae	<i>Aridius malouinensis</i>	-	-	-	-	
DIPTERA	Trichoceridae	<i>Trichocera regelationis</i>	15	0.22	1	0.02
	Sciaridae		31	0.45	8	0.13
	Chironomidae	<i>Parochlus steineni</i>	1869	27.24	39	0.66
	Heleomyzidae	<i>Prosoppantrum austrinum</i>	80	1.17	17	0.29
	Pallopidae	<i>Heloparia ekeleofi</i>	-	-	-	-
	Ephydriidae		-	-	217	3.66
THYSANOPTERA	Thripidae	<i>Apterothrips secticornis</i>	7	0.10	21	0.35
HYMENOPTERA	Mymaridae	<i>Notomyar aptenosoma</i>	139	2.02	42	0.71
ARACHNIDA	Micryphantidae	<i>Notiomaso australis</i>	1509	21.99	1681	28.34
		<i>Micromaso flavus</i>	5	0.07	75	1.26
		<i>Neomaso claggi</i>	19	0.28	26	0.44
		<i>Perimaso grytvikensis</i>	-	-	2	0.03
	Acarina	not determined	528	7.69	516	8.70
COLLEMBOLA		not determined	1666	24.28	1089	18.36
ANNELIDA	Lumbricidae		37	0.45	73	1.32
NEMATODA		not determined	6	0.09	39	0.66
TOTAL			6861		5931	
A/D/T			13.61		17.97	

2.1 Lowland communities

2.1.1 *Acaena-Tortula* community. The site was located between Grytviken cemetery and Gull Lake, near Gull Lake Stream. It was approximately 30 m above sea level and faced north. The vegetation consisted of *Acaena magellanica* with the moss *Tortula robusta* in the undergrowth. *Festuca contracta* grew sporadically in small patches at the boundary area of the site.

2.1.2 *Festuca contracta* grassland. This site was located at Susa Point at an altitude of about 50 m above sea level. It faced north-east and was in the wind shadow of Brown Mountain. Although the patches of *Festuca contracta* were closely packed, *Acaena magellanica* also occurred frequently. The whole area was very dry and felted. Dense moss cushions occupied a large proportion of the undergrowth.

At both sites, the high percentage of larvae and adults of the perimylopid *Hydromedion sparsutum* found is of considerable interest (Table 3). These animals play a key role in the ecosystems of South Georgia. The high primary production on the island is accounted for by its moist maritime climate, which includes a high amount of radiation reaching the ground (up to $7 \text{ Joule cm}^{-2} \text{ min}^{-1}$ [REMMERT 1985]), the lack of permafrost, a large amplitude of daily temperature oscillations during summertime, and a more than 6 months long growth period (REMMERT 1985). Warmblooded terrestrial phytophagous animals are absent (except introduced reindeer in some areas of the island) and the temperatures are not high enough for ectothermic phytophagous animals (REMMERT 1985). The whole turning over of the primary production takes place directly in the chain of decomposers in the soil, or else accumulates as peat. The Perimylopidae initiate the breakdown of the incoming material. Then earthworms mix the material into the soil, where it will be remineralized via springtails and mites by bacteria and fungi. In the grass-heath Perimylopidae, Annelidae, Collembola, and Acari constituted 46.21% and 63.44% (respectively) of all captured animals in 1982. Along with the increasing abundance of Perimylopidae, *Notomymar aptenosoma* (Hymenoptera, Mymaridae) also increases. Mymaridae are egg parasites (JACOBS & RENNER 1974). It is hypothesized that *Notomymar aptenosoma* parasitizes the eggs of perimylopid beetles. Carnivorous beetles (Carabidae and Staphylinidae) decrease or disappear at these sites. *Apterotherrips secticornis* (Thysanoptera) appears as a plant juice sucking insect. *Apterotherrips* is assumed to feed on *Festuca contracta*. On stands where *Festuca* covered less than 5% of the soil surface, *Apterotherrips* was not found. At Kerguelen Islands and Crozet Islands, *Apterotherrips* was collected from *Acaena-Festuca* stands too (zur Strassen, R., pers. comm.). Furthermore, *Apterotherrips secticornis* is known to occur also on Marion Island (ZUR STRASSEN 1981).

With decreasing eutrophication of the stands, the numbers of Diptera decreases. The common occurrence of chironomids (27.24% in 1982 and more than 40% in 1981) in the *Acaena* stand studied is because of the Gull Lake Stream flowing nearby. The ephydrids at Susa Point are probably blown in from coastal tussock areas. The percentage of spiders is relatively high at both sites (22.34% and 30.08% in 1982 and 15% and 25% in 1981). In the *Festuca* grassland at Susa Point four species were found simultaneously.

2.2 Altitudinal profile of Brown Mountain

To obtain more information on the vertical distribution of the epigeic invertebrate fauna we made an altitudinal profile of Brown Mountain in 1982, choosing areas at the foot of the hillside, in the middle of the slope, and at the upper boundary of the vegetation. All sites were grass-heath communities but with differing quantities of each plant species.

2.2.1 Foot of the hillside. The area was about 120 m above sea level and faced north-east. The vegetation consisted mainly of *Festuca contracta* and *Phleum alpinum*, with patches of *Acaena magellanica*. Moss undergrowth was only sparsely found. The substrate consisted of scree mixed with soil.

2.2.2 Middle of the slope. This site was about 180 m above sea level and faced north-east. The proportion of *Acaena* at this site was higher than at the previous site. Moss undergrowth was almost non-existent. The plants are rooted in a thin soil layer. On cloudy and foggy days the site may be inside a cloud layer.

2.2.3 Vegetation limit. The site was approximately 250 m above sea level. The vegetation consisted mainly of *Festuca contracta*, *Phleum alpinum* and *Acaena tenera*. *Acaena magellanica* was very rare. There were often thick moss cushions at the foot of the bare rocks.

In the profile the percentage of perimylopid beetles (larvae and adults) increased from 58.59% to nearly 67% from bottom to top, but the total number of animals trapped shows only a small increase (Table 4). Why is this so? The most dominant plant on the three sites is *Festuca contracta*. In *Festuca* stands the amount of standing dead biomass is between 70% and 85% (SMITH & STEPHENSON 1975; WALTON et al. 1975). The decomposition rate of dead *Festuca* material is very low and increases only when the material is broken down and incorporated into the soil system (WALTON & SMITH 1980). Therefore, a very important step in the nutrient cycle is to make the dead plant material available to microbial decomposition. The recycled nutrients can be re-obtained by the *Festuca* plants quickly through their mycorrhiza (Walton, D. W. H., pers. comm.) and their shallow root system (TALLOWIN 1977). The most important step is to break down the dead organic material. This job is carried out by the perimylopid beetles. Probably the nutrient cycle is extremely short in this community on very poor soil and the perimylopid beetles are the central organisms in making such a short circuit possible. With rising altitude, the percentage of *Perimylops antarcticus* increases. According to WATT (1970) *Perimylops* prefers higher altitudes because it seems to be better adapted to cold. Special searching for *Perimylops* showed, that this beetle also prefers a particular biotope structure, namely rocks covered with moss cushions overgrown with *Acaena tenera* and single *Festuca* and *Phleum* plants. Staphylinidae, Carabidae and La-

Table 4: Numbers and frequencies of invertebrates collected in the *Festuca* altitudinal profile at Brown Mountain, and the calculated numbers of animals collected per day per trap (A/D/T).

		Festuca Brown Mountain 120 m		Festuca Brown Mountain 180 m		Festuca Brown Mountain 230 m		
		№	% TOTAL	№	% TOTAL	№	% TOTAL	
COLEOPTERA	Perimylopidae	<i>Perimylops antarcticus</i>	36	0.41	87	1.04	144	2.16
		<i>P. antarcticus</i> (Larvae)	38	0.44	30	0.36	22	0.27
		<i>Hydromedion sparsutum</i>	3915	45.11	4146	49.40	4433	55.10
		<i>H. sparsutum</i> (Larvae)	1096	12.63	823	9.81	752	9.35
	Staphylinidae	<i>Halmaeus atriceps</i>	-	-	-	-	-	-
	Carabidae	<i>Oopterus soledadinus</i>	-	-	-	-	-	-
DIPTERA	Lathridiidae	<i>Aridius malouinensis</i>	-	-	-	-	-	-
		Trichoceridae	<i>Trichocera regelationis</i>	2	0.02	1	0.01	1
	Sciaridae		10	0.11	29	0.35	8	0.10
	Chironomidae	<i>Parochlus steineni</i>	7	0.08	14	0.17	20	0.25
	Heleomyzidae	<i>Prosopantrum austrinum</i>	4	0.05	-	-	65	0.81
	Palloppteridae	<i>Heloparia ekeloeffi</i>	-	-	6	0.07	-	-
Ephydriidae		1	0.01	-	-	1	0.01	
	Thripidae	<i>Apterothrips secticornis</i>	18	0.21	12	0.14	22	0.27
HYMENOPTERA	Mymaridae	<i>Notomyrma aptenosoma</i>	7	0.08	22	0.26	8	0.10
HEMIPTERA	Aphididae	<i>Jacksonia papillata</i>	-	-	5	0.06	7	0.09
ARACHNIDA	Micryphantidae	<i>Notiomaso australis</i>	1350	15.56	1283	15.29	1099	13.66
		<i>Micromaso flavus</i>	39	0.45	50	0.60	73	0.91
		<i>Neomaso claggi</i>	40	0.46	3	0.04	-	-
		<i>Perimaso grytvikensis</i>	-	-	-	-	27	0.34
	Acarina	not determined	595	6.86	593	7.07	962	11.96
COLLEMBOLA		not determined	1520	17.52	1289	15.36	401	4.98
ANNELIDA	Lumbricidae	-	-	-	-	-	-	
NEMATODA		not determined	-	-	-	-	-	
TOTAL		8678		8393		8045		
A/D/T		29.22		25.43		24.38		

thridiidae are absent in the profile. As a special feature, the occurrence of the pallopterid fly *Heloparia ekeloefi* and aphids should be mentioned. The proportion of springtails decreases with increasing altitude while the proportion of mites increases. Moisture conditions in the stands may explain this. Among the spiders, *Neomaso claggi* occurs only up to the middle of the slope where it reaches its altitude boundary. On the other hand, *Perimaso grytvikensis* is found at the higher vegetation boundary. There may be a correlation between this species and biotopes with a high amount of *Festuca*, because *Perimaso grytvikensis* is not found in tussock and marsh-bog communities.

Table 5: Numbers and frequencies of invertebrates collected in two different *Rostkovia* bogs, and the calculated numbers of animals collected per day per trap (A/D/T).

			dry <i>Rostkovia</i> bog			wet <i>Rostkovia</i> bog			
				%	TOTAL		%	TOTAL	
COLEOPTERA	Perimylopidae	<i>Perimylops antarcticus</i>	-	-	-	-	-	-	
		<i>P. antarcticus</i> (Larvae)	-	-	-	-	-	-	
		<i>Hydromedion sparsutum</i>	495	15.30		22	0.72		
		<i>H. sparsutum</i> (Larvae)	66	2.04		2	0.07		
	Staphylinidae	<i>Halmaeus atriceps</i>	2	0.06		-	-		
	Carabidae	<i>Oopterus soledadinus</i>	-	-		-	-		
	Lathridiidae	<i>Aridius malouinensis</i>	-	-		-	-		
DIPTERA	Trichoceridae	<i>Trichocera regelationis</i>	2	0.06		1	0.03		
	Sciaridae		2	0.06		2	0.07		
	Chironomidae	<i>Parochlus steineni</i>	7	0.22		1153	37.84		
	Heleomyzidae	<i>Prosopantrem austrinum</i>	14	0.43		5	0.16		
	Palloppteridae	<i>Heloparia ekeloefi</i>	-	-		1	0.03		
	Ephydriidae		46	1.42		333	10.93		
	Sphaeroceridae	<i>Archiborborus albicans</i>	-	-		12	0.39		
	THYSANOPTERA	Thripidae	<i>Apterothrips secticornis</i>	1	0.03		-	-	
	HYMENOPTERA	Mymaridae	<i>Notomyar aptenosoma</i>	1	0.03		-	-	
HEMIPTERA	Aphididae	<i>Jacksonia papillata</i>	-	-		-	-		
ARACHNIDA	Micryphantidae	<i>Notiomaso australis</i>	1177	35.45		390	12.80		
		<i>Micromaso flavus</i>	5	0.15		-	-		
		<i>Neomaso claggi</i>	1	0.03		-	-		
	Acarina	not determined	383	11.86		136	4.46		
COLLEMBOLA		not determined	995	30.81		990	32.49		
ANNELIDA	Lumbricidae		8	0.25		-	-		
NEMATODA		not determined	25	0.77		-	-		
TOTAL			3229			3047			
A/D/T			9.78			13.85			

3. Marsh-Bog Communities

In areas receiving high annual precipitation (1200–2000 mm) and melt water during the summer, there are large areas covered with marsh-bog communities. They are found on seeping slopes, on the banks of lakes and streams, or as pure bog communities with or without surface water. The array of vegetation varies from species which accompany open water (e. g. *Juncus scheuchzerioides*), to hygrophile species (e. g. *Callitriche antarctica*, *Ranunculus biternatus*, *Montia fontana*), via bog species (e. g. *Rostkovia magellanica*, *Sphagnum fimbriatum*), and moisture tolerant species (e. g. *Deschampsia antarctica*, *Acaena magellanica*). As research sites we chose a *Rostkovia* stand where the surface was dried during summer and a *Rostkovia-Tortula* bog with surface water.

3.1 *Rostkovia* stand. The sampling site was at Susa Point, on a slightly concave, sloping area. The area was moist underground (water level at a depth of 10 cm), but the surface was dry. Two plant species dominated, *Rostkovia magellanica* and partly *Juncus scheuchzerioides*. In addition, patches of *Deschampsia antarctica* and *Acaena magellanica* were found. *Phleum alpinum* and *Festuca contracta* were also found, but only in drier places on the perimeter of the site.

3.2 *Acaena*-*Tortula* bog. This site was in the Ocean Harbour area. *Rostkovia magellanica* and the moss *Tortula robusta* were the dominant plants. The whole area was covered with surface water, which originated from a melt stream of the Szielasko Ice Cap.

Each of the two types of bogs shows a distinct composition of the invertebrate fauna (Table 5). There is a large percentage of Perimylopidae in the *Rostkovia* stand at Susa Point where there is a dry surface, absent in Ocean Harbour. There are no chironomids at Susa Point. In contrast, at Ocean Harbour 38% of all collected animals were chironomids. Here we found only one species of spiders, namely *Notiomaso australis*, whereas at Susa Point there were three species. The composition of the invertebrate fauna at Susa Point seems to be obscured by animals inhabiting the drier marginal areas. Similarities of marsh-bog communities are:

1. The lack of perimylopid beetles. Carnivorous beetles such as Carabidae and Staphylinidae are absent.
2. The prominence of chironomids, which develop in water and wet moss cushions. The number of ephydrid flies is higher within the bog as they develop well in muddy areas.

Discussion

The number of terrestrial plant and animal species on South Georgia is surprisingly low. There are about 40 plant species and circa 35 invertebrate species (excluded are Acarina and Collembola). The limited size of the single "colonization islands" and the extreme isolation of the island may explain this. It is unlikely that the low species diversity is due to climatic factors alone. Compared with Arctic islands, the climate is relatively mild, even during winter, with no frost at a soil depth of 20 cm. The annual vegetation period is about 6 months long. The remarkable high level of primary production possible suggests that conditions here are suitable for the growth of higher plants, even though temperatures above 10°C are uncommon. For ectothermic animals the climate seems to be less favourable. The constantly low temperatures, together with frequent rainfall lead to a lower number of terrestrial animal species – the same process as in oceanic high arctic areas. A more detailed analysis shows that specialists, as expected, exist only in favourable habitats. Thus carabid and staphylinid beetles are restricted to warmer lowland areas, the lathridiid beetle *Aridius* is restricted to fungal hyphae in *Poa* heads, and the only parasitic hymenopteran *Notomymar* reaches a higher abundance as the number of perimylopid beetles increases. Perimylopid beetles are the most important insects in the terrestrial systems. They consume fresh plant litter, prepare it for the chain of decomposers in the soil, and attack germinating seeds. *Hydromedion sparsutum* has inhabited the island for at least 6000 years (COOPE 1963). What mechanisms of adaptation has the beetle thus far developed? The reproduction of the beetle is not strictly seasonal: all stages of development can be found simultaneously in the field. The beetles and their larvae occur mainly underground in plant litter, in the upper soil horizon and in the transition layer of "tussock stools". They thereby avoid extreme temperature conditions and do not need to develop high frost resistance or enter diapause during the cold months of the year. The beetles are active even during winter (T. Heilbronn, pers. comm.). Breeding experiments confirm these assertions. The animals' reproduction is independent of day length (MEYER-ARNDT 1984). In other insect species also all stages of development can be found simultaneously living in the field, without a distinct seasonal rhythm. Compared to the prominent status of the beetles, the other insects are only of secondary importance. Thus, in spite of major differences in plant communities, the same insect community is dis-

tributed all over the investigated sites. Clear differences, consistent from two years, are found in relative frequencies of species at different sites, rather than in species composition. But even if the species composition is different – as in the different “islands” of South Georgia – the principal picture remains constant: Degradation of primary production (and, to a certain extent, feeding on seedlings) is achieved by the beetles of the perimylopidae family. Instead of the northern midges *Hydromedion sparsutum* and *Perimylops antarcticus* play the major role. Even the sciarids, probably introduced, seem to be unable to outcompete the beetles.

There is virtually no pollination by insects on South Georgia. No flower attracting insects can be found; at most, accidental pollination by Collembola or cross-trekking by beetles (R. I. Lewis Smith, pers. comm.) may be possible. Even the shining flowers of the introduced *Taraxacum* around the Grytviken cemetery do not attract any South Georgian insects. A great number of flowers collected revealed no insect within them.

Even the predator system is very different from northern areas. Only in the climatically milder areas live predatory carabids and staphylinids, and their occurrence and number are similar to arctic areas. The important ichneumonid parasites are almost completely missing. Whereas on Spitzbergen these parasites can make up more than 20% of the total catch of winged insects (HINZ 1976) and spiders, there is only one species (*Notomyrma aptenosoma*) on South Georgia, which probably parasitizes eggs of perimylopidae beetles, and is exceedingly scarce all over the island – regularly found only in very dense populations of perimylopids. On the other hand, spiders are of marked importance. They can make up 13% to 36% of the collected invertebrates, whereas their proportion on Spitzbergen is only 4.5% (HINZ 1976) and in Central Europe in comparable collections they have a proportion between 2% and 13% (NENTWIG 1982).

The faunal composition of the South Georgian tundra and thus the structure and function of the different systematic groups is very different from the arctic tundra regions. Only the very general principles remain common: the lack of ectothermic herbivores and the very broad ecological niche of most members of the polar fauna.

Acknowledgements

Grateful acknowledgement is made to the British Antarctic Survey for providing the opportunity to work on South Georgia. Special thanks go to my colleague Volker Nicolai and to all members of the station at King Edward Point on South Georgia for their unlimited help. For support during the research and comments on the manuscript, I am very much obliged to Prof. Dr. Remmert. Identification of the spiders was conducted by Stefan Heimer (Dresden) and fly identification was carried out with the help of Dr. v. Tschirnhaus (Bielefeld), whilst *Trechisibus antarcticus* was identified by Dr. M. Baehr (München). Thanks is also extended to Craig W. Graver for help with the translation and to Julie Hamilton for corrections of the manuscript. The financial assistance for this research was provided by the Deutsche Forschungsgemeinschaft.

References

- COOPE, G. R. 1963: The occurrence of the beetle *Hydromedion sparsutum* (Müll.) in a peat profile from Jason Island, South Georgia. – Brit. Antarct. Surv. Bull. 1: 25–26
- DAHL, C. H. 1970: Diptera: Trichoceridae of South Georgia. – Pac. Ins. Monogr. 23: 271–273
- FORSTER, R. R. 1970: Araneae: Spiders of South Georgia. – Pac. Ins. Monogr. 23: 31–42
- GREENE, S. W. 1964: The vascular flora of South Georgia. – Brit. Antarct. Surv., Scient. Rep. 45: 1–58
- GRESSITT, J. L. (ed.) 1970: Subantarctic entomology, particularly of South Georgia and Heard Island. – Pac. Ins. Monogr. 23
- HINZ, W. 1976: Zur Ökologie der Tundra Spitzbergens. – Nor. Polarinst. Skr. 163: 1–47
- JACOBS, W. & RENNER, M. 1974: Taschenbuch zur Biologie der Insekten. – Gustav Fischer Verlag Stuttgart, 1–635
- LAWS, R. M. 1978: Ecological studies on South Georgia. – S. Afr. J. Antarct. Res. 8: 3–13

- MEYER-ARNDT, S. 1984: Growth and Development of *Hydromedion sparsutum* (Müller) (Coleoptera, Perimylopidae) from South Georgia at Different Temperatures. – *Polar Biol.* **3**: 73–76
- NENTWIG, W. 1982: Epigeic spiders, their potential prey and competitors: Size and frequency relations. – *Oecologia* (Berl.) **55**: 130–136
- REMMERT, H. 1980: Arctic animal ecology. – Springer-Verlag, Berlin Heidelberg New York, 1–250
- — 1985: Spitzbergen und Südgeorgien: Ein ökologischer Vergleich. – *Natur und Museum*, **115**: 237–249
- SMITH, R. I. L. & STEPHENSON, C. 1975: Preliminary growth studies on *Festuca contarcta* T. Kirk and *Deschampsia antarctica* Desv. on South Georgia. – *Brit. Antarct. Surv. Bull.* **41/42**: 59–76
- SMITH, R. I. L. & WALTON, D. W. H. 1975: South Georgia, Subantarctic. In: ROSSWALL, T. & HEAL, O. W.: Structure and function of tundra ecosystems. – *Ecol. Bull.* (Stockholm) **20**: 399–423
- TALLOWIN, R. B. 1977: The reproductive strategies on a subantarctic grass, *Festuca contracta*. – In: LLANO, G. A. (ed.): Adaptations within Antarctic ecosystems. Houston, Texas, Gulf Publishing Company, 967–980
- VOGEL, M. and NICOLAI, V. 1983: The invertebrate fauna of the old whaling station Grytviken/South Georgia. – *Polar Record* **135**: 607–609
- WALTON, D. W. H., GREENE, D. M. & CALLAGHAN, T. V. 1975: An assessment of primary production in a subantarctic grassland on South Georgia. – *Brit. Antarct. Surv. Bull.* **41**: 151–160
- WALTON, D. W. H. & SMITH, R. I. L. 1980: The chemical composition of South Georgian vegetation. – *Brit. Antarct. Surv. Bull.* **49**: 116–135
- WATT, J. C. 1967: The families Perimylopidae and Dacoderidae (Coleoptera, Heteromera). – *Proc. Roy. Ent. Soc. (B)* **36**: 109–118
- — 1970: Coleoptera: Perimylopidae of South Georgia. – *Pac. Ins. Monogr.* **23**: 243–253
- ZUR STRASSEN, R. 1981: On Thysanoptera (Insecta) from some islands in the subantarctic part of the Indian Ocean. – *C.N.F.R.A.* **48**: 159–169

Michael Vogel,
 Fachbereich Biologie/Zoologie
 Philipps Universität Marburg
 P. O. Box 1929
 D-3550 Marburg/Lahn